

II. *Notes upon, or suggested by, the colours, markings, and protective attitudes of certain lepidopterous larvæ and pupæ, and of a phytophagous hymenopterous larva.* By EDWARD B. POULTON, M.A.

[Read November 7th, 1883.]

PLATE I.

IN the following notes I have numbered the segments of larvæ according to the general custom of English entomologists. The head is considered as the 1st segment, and the others are counted (antero-posteriorly) from two to twelve. In adopting this plan I simply wish to be intelligible, and do not stand committed to any theory. I wish to express my sincere thanks to Prof. Westwood for his kind help and advice in this as well as in all other work that I have done in Entomology.

THE MARKINGS OF SOME LARVÆ OF THE GENERA SMERINTHUS AND SPHINX.—The following notes were made after reading Professor Weismann's most interesting and suggestive Essay on 'The Origin of the Markings of Caterpillars,' together with Mr. Meldola's important additions to the English translation. Some observations I have to record were made during the past summer (1883). In other cases (which will be indicated) I have been obliged to rely on my memory for facts of which I did not see the significance at the time when they were noticed, and to which therefore I did not direct very careful attention. This will explain some deficiency of detail in certain observations, although in such cases the main facts have been firmly impressed upon my recollection.

1. *The red spots that sometimes occur on Smerinthus larvæ.*—Weismann considers that this well-known variation represents a step in the origin of coloured borders to the oblique stripes such as are met with in *Sphinx*. I have never been fortunate enough to find these spots in *S. tiliæ*, although the larva is well known to me. This is all the more unfortunate, because Weismann's conclusions have

been chiefly formed from the study of this species. But I have been long familiar with the coloured spots upon larvæ of *S. ocellatus* and *S. populi*, and I am perfectly convinced that, in these species at any rate, they have nothing to do with coloured borders to the oblique stripes. It is quite possible that they afford protection by resembling galls:—seen irregularly, as they are, between the leaves and upon a ground colour very much like the under side of the leaves (see the Editor's notes to the translation of Weismann's book). But I do not think that we can yet speak of their significance with any certainty. The spots are excessively variable in size, in the number found in each row, and in the number of the rows themselves. In these facts we do not seem to recognise the slow but sure accumulation of favourable variations by natural selection. I think it is probable that we see the decline of an old rather than the establishment of a new character. In fact the extreme variability of the spots, when present, seems to be best explained by reversion, which is often unequal and irregular in its action. It should also be remembered that a decided majority of the larvæ of *S. populi*, and an immense majority of *S. ocellatus*, have no trace of these markings.

Shortly after reading Weismann's Essay I was fortunate enough to find a spotted variety of *S. ocellatus* (August 18th, 1883). The larva was feeding on *Salix cinerea* by the banks of the River Cherwell. It had the bright yellowish green ground colour, and each of the spiracles was, as usual, encircled by a fine red line. The following is an account of the number and arrangement of the spots (see Pl. I., fig. 1):—Each of the spiracles of segments 5 to 11 (inclusive) was upon or near a red patch, very slightly indicated on segments 5 and 11, and not greatly developed on the others. Except in the smallest instances, each spot was made up of two patches, one anterior and the other posterior to the spiracle, with its encircling red line. There was also a row of spots above and below that just described, and the spots of both were approximately alternate with those of the latter, and therefore each spot of the highest row was situated vertically over one of the lowest, as far as the two rows corresponded. There are only four spots in the lowest row (on each side of the body), one upon each of the first four claspers; while in the highest row there are distinct spots on the 7th,

8th, 9th, and 10th segments, and a very slight one on the 6th segment, and on the 11th of the right side only.

Thus the spiracular row contains the greatest number of spots, but I believe that the highest row is generally best developed, especially in the size of the spots.

It seems perfectly obvious that we have (here at least) markings which bear no relation to the coloured borders of the oblique stripes. We have a system of three rows whose spots form alternating series, and only the spots of the highest row are placed in front of the oblique white stripes, in the position of the coloured borders found in the genus *Sphinx*. And the highest spots show no tendency to become drawn out into oblique lines. One spot only, and that belonging to the spiracular row, communicates a faint tinge of red (not shown in the figure) to the last white oblique stripe; but this tinge shows no tendency to separate as an anterior coloured border, and the spot which communicates it is placed *behind* the oblique stripe. These observations and conclusions are also entirely in accordance with what I remember of the spotted varieties of these two larvæ. At the same time a darker shade of the ground colour forms a very distinct border to the anterior edge of each oblique white stripe, and greatly increases the efficiency of the protective resemblance to leaf-veining.

I shall presently show reasons for the belief that the coloured borders of *Sphinx* correspond to these green edges, which are distinct in all larvæ of *Smerinthus ocellatus*, whatever be the shade of the ground colour.

Since writing the above I have seen figures of the spotted variety of *S. tiliæ*. The spots certainly show a great tendency to become drawn out into stripes in this species, but such a tendency does not seem to be general in this form of marking, for it is not exhibited in *S. populi*, in which the spots are often developed to an extent never reached by *S. tiliæ*.

Through the kindness of Mr. G. C. Bignell, who has lent me his original painting for the purpose, I am now enabled to add a figure of an extreme variety of *S. populi*. This is shown in Pl. I., fig. 2, and the specimen is remarkable for its very light ground colour, as well as for the unusual development of the spots. Although the spots are developed to a greater extent, especially anteriorly, than in any specimen I have found, yet

varieties approaching fig. 2 are not uncommon. The alternate arrangement is not marked to the same extent as in fig. 1, and the spots are not greatly developed upon the claspers. Anteriorly the spots are not distributed regularly upon the segments, since the former exceed the latter in number. This fact brings out very clearly the want of relation to the oblique stripes, for these are not developed at all anteriorly, and the remnant of the subdorsal, which follows the oblique line system (as will be shown) in the chief protective attitude, sweeps over the contracted anterior segments as a whole without any suggestion of a separate development upon each of them. In fact, a development of oblique lines on each small anterior segment, approaching the development of the spots, would destroy the symmetry and protective value of the whole system. In fig. 2 there is no tendency towards a drawing out of the spots into lines, except perhaps to some extent in connection with the 7th stripe, as was also shown in fig. 1; and this slight tendency does not appear to be in the direction of forming anterior coloured borders. It seems possible that in *S. tiliæ* there is a further intensification of the tendency shown in the 7th stripe of *S. ocellatus* and *populi*, and that there is no relation to coloured borders such as are met with in *Sphinx*.

If *S. tiliæ* is developing after the manner suggested by Prof. Weismann, and *Sphinx ligustri* has lost the spot-stage in its ontogeny, it must nevertheless remain true that *S. ocellatus* and *populi* have progressed in quite another direction. But, considering the above facts and those which follow, it seems more probable that *S. tiliæ* occasionally presents us with a modification which renders its own oblique striping more distinct by a suffusion with the colour of the spots, but that this has no significance for the coloured borders invariably present in *Sphinx ligustri*, &c., which arise directly from the darkened ground colour anterior to the light stripes. Such an extreme instance of this variety as is shown in fig. 2, coexisting with a vast majority of larvæ (of the same species) without a trace of the marking, seems to be greatly in favour of the view that the whole character is due to occasional reversion to a form of marking which is disadvantageous to larvæ protected by their resemblance to leaves. The theory of protection by resemblance to galls is not supported by such a complete

system of spots as is shown in fig. 2, and it is further rendered unlikely by the fact that *S. populi* presents the variety far more commonly and to a far greater extent than *S. ocellatus* (considering the relative abundance and arrangement of galls upon the leaves of their respective food-plants). The spotted varieties are certainly more conspicuous than the others, and such a variety as fig. 2 is very much more conspicuous. Not only is this true, but the modification of the spots, suggested by Professor Weismann, would also be disadvantageous in rendering the larva conspicuous, and *Sphinx ligustri* is far more easily detected than the *Smerinthus* larvæ. The protective resemblances, in fact, belong to two different classes (as will be pointed out), for *S. ocellatus* resembles a rolled-up leaf (at any rate when feeding upon apple), while *S. ligustri* is protected by a general harmony with its surroundings. Hence the coloured borders would be disadvantageous in the former case, as they would destroy the special resemblance; while they may be beneficial in the latter case, where the resemblance is to a general effect caused by complex combinations of light and shade falling upon a large and heterogeneous object. And so also with *S. tiliæ* and *populi*, which are protected by a special resemblance to leaves or parts of leaves.

2. *The origin of the white stripes in Smerinthus.*—If the shagreen dots be carefully observed they will be found to possess an annular arrangement. There are generally eight rings in the largest segments. As each ring intersects a white stripe (either belonging to the oblique or subdorsal system), the dot that is placed upon the stripe is much larger than others near it in the same ring. The largest oblique stripe—the last—has more than one row of dots. When the full-fed larva has ceased to feed, and is lying quiescent in a contracted state before pupation, the colours are much changed. The white striping disappears, and the ordinary shagreen dots become very inconspicuous, but the enlarged dots remain distinct, and thus the whole system of lines can at once be recognised. It is thus seen how large these dots really are, for under other conditions they are hard to detect, being placed on a white ground. In addition to their arrangement upon the usual stripes there is a line of enlarged dots on each side of the dark pulsating dorsal line formed by the dorsal vessel. In this case the ground colour has not become white along the line

of dots. These facts seem to indicate that the white lines of the larva first arose as enlargements of the shagreen dots, and that the effect has been increased by the ground colour becoming gradually lighter along the same lines. The extreme anterior end of the subdorsal seems to be made up of a row of dots only, without any whitening of the ground colour. The dots on each side of the dorsal line doubtless serve to render the latter more distinct. The importance of the dorsal line is very great for protective purposes, as it represents the midrib of a leaf. It is possible that the ground colour may now be in process of change along these two lines. At the same time the changes of colour before pupation afford evidence that the dark anterior borders to the oblique stripes have risen to the position of distinct and independent markings, and are not merely local deepening of the ground colour. At the time I speak of, the ground colour fades and is replaced by dirty brown, but the green borders appear more distinct than ever (in some specimens at least, and in none do they share the fate of the ground colour). It is very probable that the origin of the white markings from the shagreen dots can be proved in the ontogeny.

3. *The use of the remains of the subdorsal in the last stage of Smerinthus.*—At this stage the subdorsal line remains distinct (as Weismann points out) in front of the oblique stripes, and also intersects the first two or three of these, gradually disappearing posteriorly. I believe that it is not generally known that there is the beginning of an 8th oblique stripe, slightly marked, on the 5th segment (see figs. 1, 3, and 4). This stripe (which possesses a dark coloured anterior border remaining after the changes before pupation) begins superiorly at almost the same level as the others; inferiorly it reaches, but does not cross, the subdorsal. If the oblique stripes were repeated anteriorly, with the same relation to the segments that they bear to those where they are present, they would entirely mar the effect of a series, because the anterior segments are so much smaller than the others, and are, further, much contracted when the larva most needs the protective resemblance, *i. e.*, when it is at rest and assuming the *Sphinx* attitude. But, if a larva be watched in this position, it will be seen that the subdorsal line, following the curved anterior segments, becomes approximately parallel to the oblique stripes

(Pl. I., fig. 4). The effect is heightened by the slight oblique stripe on the 5th segment, for the eye naturally regards this as the true continuation of the subdorsal. The curving and contraction of the anterior segments do not produce perfect parallelism, but quite enough for the eye to accept the subdorsal as part of the series of oblique stripes. It is an instance of an imperfect suggestion being sufficient to continue a series of markings, and to be efficient in protection. I have no doubt that this is the cause of the retention of the anterior part of the subdorsal and of its gradual disappearance posteriorly. When the larva is at rest the contraction of the anterior segments is so great that the spiracle on the 2nd segment is always partially and sometimes completely hidden. Fig. 4 shows the attitude of rest, but the same larva as that drawn in fig. 3 has been here given, and the subdorsal is in consequence less subordinated to the oblique stripes than is usually the case.

The same adaptation of an older system of markings to a more recent oblique line system is seen in other larvæ, as well as in the *Sphingidæ*. Thus, in the larva of *Endromis versicolor*, as depicted on page 203 of Newman's 'British Moths,' a distinct dorsal line is drawn, and another line, which appears to be spiracular in the 2nd segment and subspiracular in the 6th. There is also the oblique line system consisting of eight stripes (which slope in the opposite direction to those of *Sphingidæ*) upon segments 4—11 inclusive. The spiracular line is distinguished by a longitudinal row of dots, as well as by its position. It appears to be normal in segments 2—6, but on the 7th segment it becomes oblique, and forms a continuation of the true oblique stripe on the 6th segment. This is also the case upon all the segments up to and including the 12th. In each case the true oblique line upon one segment is continued posteriorly on to the next segment by a modification in position of the subspiracular line upon the latter. Although modified, the subspiracular oblique lines retain their characteristic dots, and it is thus easy to recognise this portion of the stripe as belonging to a different system, which is retained unchanged anteriorly. This is therefore an extremely interesting adaptation of an older to a newer form of marking, which has taken place where the latter is chiefly developed (after the 6th segment).

The larva thus represented is certainly adult, and I

have tried, but without success, to find figures of the younger stages. I have no doubt that in the early stages the horizontal system is alone present, and that later these lines coexist with an oblique system, while in the highest stage the former becomes part of the latter. In fig. 5 a copy is given of the larva represented upon page 203 of Newman's 'British Moths.'

4. *The comparatively recent replacement of the subdorsal by the oblique lines in Smerinthus.* — Weismann proves this fact from the ontogeny of the larvæ.

After the formation of the oblique line system it seems likely that the subdorsal somewhat rapidly disappeared from all but the anterior segments of the adult larva, because (as Weismann points out) it would interfere with the protection from the oblique lines, and also because it would spoil the effect of its anterior part, which, as above shown, lends itself to the newer system of markings. But these changes must have been very recent, for traces of the subdorsal can generally be made out by careful observation upon all the usual segments in adult larvæ.

In the gradual deepening of the ground colour to form the borders to the oblique white lines the point of intersection of the former with the white subdorsal must have been lighter than the ground colour, and has therefore taken longer to darken. Hence in each segment, at the level of the posterior part of the subdorsal remnant, a light linear interruption of the green border can generally be detected. In one adult larva, with the bluish green ground colour (found on *Salix viminalis* by the River Cherwell, Sept. 8th, 1883), these light short lines were connected together into a faint representation of a complete subdorsal line, ending posteriorly in the last white stripe (see fig. 3). The line was here most distinct and linear where it crossed the dark borders, but was fairly well-defined inferiorly through its whole length. The upper limits gradually shaded off into the ground colour, and the line seemed to spread upwards in the anterior part of each segment, so that it was of considerable thickness where it joined the white oblique line. But this appearance can be detected in the posterior part of the subdorsal remnant in most larvæ. The larva which thus retained the subdorsal was full-fed and of large size. This observation shows (together with the traces which can often be detected) that the

subdorsal has been retained very late in the phylogeny of the genus *Smerinthus*.

5. *The probable phytophagic character of the ground colour in S. ocellatus.*—This conclusion is suggested by Mr. Meldola in the notes to his translation of Weismann's book. I have no doubt that experiment will settle the question in the affirmative. In the meantime I give a list of the trees upon which I have found *S. ocellatus* during the past summer, with the colour of the leaves (under sides) and the larvæ. The invariable resemblance of the latter to the former in many species of plants is much in favour of the cause being phytophagic, unless we imagine that the larvæ are truly dimorphic, and that the moths of each variety lay their eggs on the appropriate trees only. I have found the bright yellowish green variety on *Salix cinerea* and *S. rubra*, and formerly, I believe, on a crab-apple tree at Reading. The under side of the leaves of the crab are whitish, but brighter in appearance than those of other apples, which have a peculiarly "dead" colour very characteristic of the whitish green larva. I have found the latter upon *Salix viminalis* and commonly upon apple (see Mr. Meldola's note on the subject).

6. *Protection sometimes gained by the changes in colour before pupation.*—The adult larva of *S. tiliæ* turns a dark purplish brown before pupation, and has usually assumed this tint by the time that it has come down from the tree upon which it was feeding. The same is true of *Sphinx ligustri*, which becomes quite brown on the back, and in this condition may often be found hurrying along a road or garden path in search of a suitable place to bury itself. I have found a larva of *S. ligustri*, still upon its food-plant, with distinct indications of the brown colour.

In these two species the dark coloration before the final change is very marked in amount and very early in appearance. Conversely the larvæ of *Smerinthus ocellatus* and *S. populi* show but a slight tinge of brown when they have left the trees and are wandering about before burying themselves. In all these cases I am speaking of the change of colour in the full-fed larva when it ceases to feed and makes preparation for the final change: I do not refer to the colours (already described in *S. ocellatus*) assumed in the quiescent condition immediately preceding pupation.

Contrasting the conditions of these larvæ, which behave so differently before pupation, we observe that the chief food-plants of *S. ocellatus* and *S. populi* are sallow and poplar respectively, and that these almost invariably grow in damp situations, and are surrounded by grass or other green vegetation. Thus the original ground colour of the larvæ is the best protection under such circumstances, and, in fact, it is very slightly altered. But the food-plants of the other two larvæ (elm and lime for *S. tiliæ*, many plants for *Sphinx ligustri*, e.g., privet, lilac, laurustinus, syringa, ash, holly, &c.) do not grow in damp places, and are generally surrounded by the bare ground or short turf. Hence, I believe, the importance of the darkening in these instances. In the case of a very large brightly coloured larva like *Sphinx ligustri*, which would show up as an extremely conspicuous object against the ground, this time of moving rapidly about before burying would indeed be fatal.

It is probable that the brown or dark shades so often met with before pupation are due to changes taking place in the larval colours, and are merely incidental to their destruction. Natural selection would then in certain cases seize upon the slight incidental darkening, and would give it such determinate direction as we see in *Sphinx ligustri*, &c. It is probable, too, that the same agency would diminish and retard the darkening in cases where it is unfavourable.

This explanation is probably correct, if we grant the extreme danger of this period to larvæ when they descend from their food-plant and come within the reach of new foes as well as old.

7. *The relation of the markings of Sphinx to those of Smerinthus.*—There is one fact in the ontogeny of *S. ligustri* which I think is not recorded by Weismann, that the larva is covered with white shagreen dots, until (I believe) the last ecdysis. I am almost certain that the shagreening is retained up to this point, although I have not seen it for many years. The shagreen is exactly like that on *Smerinthus* larvæ, and the retention of this character in the earlier stages of *Sphinx* is a very strong argument for the later origin of the latter, and from a form possessing likeness to *Smerinthus*. I believe that in the younger stages the oblique stripes also resemble those of *Smerinthus* in the character of

the white lines, and in the presence of borders formed by a deepening of the ground colour. The pure white stripes only appear when the skin becomes smooth, but before this the purple borders can be seen, although narrow and not conspicuous. I do not remember any indications of spots which gave rise to the borders by coalescence, but I believe that the latter took the place of the dark green edges.

The above statements are from memory: I can now speak with certainty as to the last stage, for I have carefully examined several specimens after reading Weismann's book. The beautiful delicate white stripes still retain indications of the shagreen covering in their anterior inferior extremities, which are made up of scattered white points. Superiorly and posteriorly they still show traces of their origin from stripes, resembling those of *Smerinthus*, for, continued on to the segment behind that in which most of its course lies, the white stripe becomes of a pale yellowish green, and can be followed nearly up to the dorsal line (formed by the dorsal vessel). The recognition of this superior continuation needs close observation, but it will be readily seen now that attention is directed to it. At the same limit the purple border to the white stripe changes superiorly and posteriorly into a dark green border to the yellowish stripe. This also continues nearly up to the dorsal line, and can be recognised with a little attention (see fig. 7). These observations seem to prove that the purple border has been modified from a dark green border (like that of *Smerinthus*) at the sides, but not above, where the latter faintly persists. In the same manner the pure white stripes have arisen from lines, like those of *Smerinthus*, which still remain above. The relation between the bright colouring of *Sphinx* and the obscure colouring of *Smerinthus* is very well seen by looking carefully at an adult *Sphinx ligustri* from above (see fig. 6).

These last facts, together with the marking of earlier stages and the long retention of shagreen, prove that the beautiful colours of *Sphinx ligustri* have been acquired very late in the phylogeny.

8. *Further notes on the adult larva of Sphinx ligustri.*—The anterior spiracle (on the 2nd segment) is not hidden during rest, although the *Sphinx* attitude is so marked in this genus. I found one specimen of *S. ligustri* (at Wootton, near Oxford, Sept. 14th, 1883)

which showed some interesting facts in connection with the oblique stripes. In the first place the tendency towards the repetition of markings in segmented animals had shown itself in the appearance of a slight oblique stripe on the 12th segment. This was very nearly parallel with the others, and consisted of an interrupted purple line, with the white stripe only indicated by a few isolated points at the lower end of the purple line (see fig. 7). This imperfect repetition of the oblique stripes occurred on both right and left sides, but without complete symmetry.

Another interesting fact was that the purple borders of the seven usual stripes became darker at about the middle, and this gradually increased until the lower end was very nearly black. The dark colour was repeated on the other side of the white stripe as an irregular patch opposite to the inferior end of the purple border. The darkening of the border began at the anterior edge and gradually extended posteriorly until in the lower quarter of the purple stripe it had affected its whole thickness (see fig. 7, in which the darkening is not sufficiently indicated). The dark patch behind the lower end of the white stripe was almost or completely hidden when the segments were at all contracted.

PROTECTIVE ATTITUDES IN THE LARVÆ OF GEOMETRÆ.—During the present year (1883) I have reared from the egg, larvæ of the three less-known species of *Ephyridæ*, *Ephyra pendularia*, *E. orbicularia*, and *E. omicronaria*. Although the perfect insects are well known, I infer that the larvæ are seldom seen, from the meagre descriptions in text-books, and from the fact that the food-plants are quoted from Guenée by both Stainton and Newman. My object was to experiment upon the pupæ in order to investigate the causes of seasonal dimorphism in this group of moths, using Prof. Weismann's methods (see the translation of his book on this subject by Meldola). I therefore directed no especial attention to the larvæ, being very busy with other work at the time; but upon one occasion I found the larvæ of *E. pendularia* assuming a remarkable spiral attitude which I had never before observed. This caused me to observe more closely, and ultimately led to the following notes.

The larvæ of *Geometræ* are especially protected, as is well known, by their resemblance to twigs and thorns which stand out straight from a stem, generally making

an acute angle with it. Accordingly the larvæ in nearly all cases tend to assume this position when at rest, and the resemblance is often carried further by the presence of roughnesses and tubercles on the larvæ exactly like those on a twig. The usual brown colour of the caterpillar may even have a slight green dusting in places (*R. crategata*) indistinguishable in appearance from the lichenous growth with which bark is generally covered in damp situations. A practised entomologist has often to touch a larva before he is sure that he is not looking at a twig; and he may often at the first glance mistake the one for the other, when the larva is shaken from its hold and falls, still perfectly rigid, into the beating-tray or umbrella. And the protection is far more complete when the larva clings to a branch of its food-plant. These facts are well known to every collector of insects: it is their limitation which I believe has been less noticed. This characteristic protective attitude is especially applicable to larvæ feeding on the leaves of trees, and would not be nearly so effective for those feeding on low-growing plants of which only a tuft of leaves is apparent above the ground. It may be safely assumed that the usual attitude would even be dangerously conspicuous for any fair-sized Geometer larva (unless green) which rested by day on the leaves of its food-plant. Thus the larvæ of *Aspilates citraria* and *A. gilvaria* have the habit of coiling up the anterior part of the body vertically into a flat spiral, with the head in the centre. If shaken from the food-plant the attitude is maintained. In this case the resemblance to a small bleached snail-shell is very striking, both in shape and colour. The situation which the larva frequents is exactly that where small empty shells are found in abundance, and all the localities I know of in which these moths are common are upon limestone, which is also favourable to the presence of these mollusca.

Two points about this protective attitude are of great interest, firstly, that the position when assumed upon the food-plant is just as dependent upon the normal structure of a Geometer larva as the more usual attitude of resemblance to twigs, &c. Secondly, that the object resembled is a dead and bleached shell; for it is very likely that many enemies of the larva (birds, &c.), would not object to a living snail, and the resemblance might thus be no protection if the pale colour did not coexist with the spiral posture.

There is also a period in which the usual attitude must be dangerous to Geometer larvæ feeding upon trees. I refer to the time when the young larva feeds and rests *upon* the leaf and does not retire to the stem. At this time the rigid position and the attenuated body attached by the posterior end to the surface or edge of a leaf would tend to attract attention. At the same time it is likely that larvæ have, as a rule, most to fear, in these early stages of growth, from their deadliest enemies, hymenopterous and dipterous parasites. These parasites appear on the wing, as far as I have observed, at the same time as the lepidopterous imago, and therefore it is probable that the larvæ in which their eggs are laid must be very young. Further, when larvæ possess a special apparatus for driving away Ichneumons, &c., the protective structures are well developed in early stages.

Indeed, in *Dicranura vinula* the protrusible flagella are of the greatest relative size in the young larva, and gradually become of less importance during growth, until it is rare to find the structures of any functional value in a larva much more than half-grown. In nearly all cases the flagella have ceased to be protrusible before the larva is full-grown. This follows from natural causes, and holds good when the structures have not been injured by other larvæ of the same species.

Of course the need of protection from birds remains through life, and is doubtless more necessary as the size of the larva increases and renders it more conspicuous. But in early stages there is the additional need of protection from parasites.

The objects usually met with upon leaves have an irregular shape, with a frequent tendency towards the spiral form. Such are, parts of the leaf accidentally injured and curled up, spiral or imperfectly cylindrical cases formed by many larvæ, the excrement of birds and snails. Nothing could be more unlike the usual attitude of a Geometer larva. As to colour, the leaf-fragments and larval cases are brown, the excrement of snails dark, while that of birds is rendered conspicuous by irregular white patches on a dark ground. Of course the usual attitude can be retained by larvæ of a green colour, for these would be almost invisible against the background of the leaf. It was very interesting therefore to find the green larvæ of *E. omicronaria* in the normal position whenever I observed them. I cannot be sure that they

never rested in another posture, but I am certain that this was not commonly the case. Next year I hope to be able to settle the point by further and more extended observations.

When the larvæ of *E. pendularia* were about half the full size, and brown in colour, I observed that they were, with hardly an exception, hanging from the under side or edges of the leaves, and that the body was thrown into a spiral of from one to one and a half turns. The head was nearly always downwards, and the caterpillar greatly resembled a brown spiral larva-case hanging from a leaf,—in fact, I thought for a moment that some of these must have been accidentally introduced with the food. I afterwards found that this was a common attitude during rest, and that it was especially maintained during the long period of quiescence that precedes ecdysis. It was so continuous on this latter occasion, and occurred in so many larvæ (I did not notice a single exception), that I thought for a long time that it must be important in producing tension in the old skin. But the attitude occurs at other times, and further, I have never noticed it in other larvæ before ecdysis, where the same tension would be as beneficial as in this case. If the object of the spiral attitude be to split the old skin we should expect to see it assumed just before ecdysis, and not maintained for the long period during which the larva ceases to feed. If further observations show that this position is of assistance to ecdysis it will still be true that the larva derives other benefits, in the same way that the usual darkening of colours before pupation is also of protective importance when larvæ wander over the ground in search of a spot to bury in. But, as far as my observations have gone at present, I am inclined to think that this attitude is especially maintained on such occasions, because the larvæ are then necessarily quiet, and have no reason to give up the protective position. These periods are the only long rests of larval life during which protection of attitude (as apart from colour) can be uninterruptedly kept up, for at all other times there is the constant necessity of feeding and of moving to fresh food, although the danger is frequently averted by such movements being nocturnal.

The larvæ of *E. pendularia* assume the normal attitude of *Geometræ* after the last ecdysis, and then usually

cling to the branches. They are at this stage dimorphic, the more numerous being green, while the others are brown. The latter are protected by their resemblance to twigs, the former by their likeness to young green shoots, and by being invisible against the background of leaves.

The larvæ of *E. pendularia* emerged from the eggs before those of the other two species, and fed up far more rapidly. I was therefore able to watch the other larvæ during the whole period in which protective attitudes are assumed; for the chief protection at the earliest stage (I mean before the first ecdysis) must be the extremely small size and the absence of conspicuous colours or markings. I have already mentioned that I never observed the green larvæ of *E. omicronaria* in any other than the normal attitude. After the last change of skin these larvæ also become dimorphic, but the brown variety forms a very small proportion in this case (one out of twelve larvæ). Before the last stage all these larvæ were green.

The larvæ of *E. orbicularia* were dark-coloured when young, and very early took up a position in which they exactly resembled snail's excrement. The body was twisted into a very irregular spiral (far more irregular than in the case of *E. pendularia* when observed). The illusion was all the more complete, because at this stage the leaf was eaten from the surface and not from the edge, and thus the chief strands of the fibro-vascular framework were left, exactly as they are when a snail has been at work. When the larva becomes larger it presents, when at rest, a striking resemblance to the excrement of birds. It is still dark-coloured, but possesses a series of white markings along the sides, which are shown irregularly in the twists and curves of the attitude assumed. A common position at this stage (when about half-grown) is a spiral twist of about one turn, from the posterior end as far as the last pair of true legs, and then at this point a sudden bend backwards of the anterior segments and head to a right angle with the proximal posterior segments. The effect is highly irregular. From some points of view the appearance is that of another smaller turn added to the first.

In larvæ which habitually assume an apparently angular position it is very common for the bends to be marked by a tubercle or prominence on their convex side. Thus the bends, pointed in this way, appear to be much sharper than they really are,—in fact they look

like angles, but are really bends. This effect is produced in the larva of *E. orbicularia* by thrusting out the posterior pair of true legs, which are situated on the convex side of the bend I have described. The spiral attitude is also chiefly maintained during the long rests before ecdysis, and is usually abandoned when the larva is nearly full-grown, although tendencies towards the habit are then occasionally observed.

When the larvæ are disturbed they resort to other methods of protection; first letting themselves down by a thread, and, if further irritated, falling to the ground and wriggling with great rapidity for some time. This habit is also followed by *E. pendularia* and *E. omicronaria*, and it is common in many larvæ. The rapid movements seem obviously directed towards escape from insect-parasites, but it might also be useful in working the larva down among the roots of grass, &c. But the remarkable thing about the two species of larvæ mentioned above is that these bilaterally symmetrical animals should sometimes assume an asymmetrical position when at rest. The best instance of such attitudes that I have seen was pointed out to me by Professor Westwood, *i. e.*, some of the *Phasmidæ*, which, resembling branches with lateral twigs, hold their limbs asymmetrically, thus increasing the protective likeness. But I have not before observed any departure from bilateral symmetry in the various protective attitudes of lepidopterous larvæ. It seems very likely that this habit will be found during young stages of other Geometer larvæ, unless protected by a green colour, or in some other special way. It is possible, however, that the habit is confined to the *Ephyridæ*, or specially manifested by them, as this family in some respects stands alone among *Geometræ*. Since writing the above I have been told of other instances, and have also found some myself. In all cases the asymmetrical attitude appears in Geometer larvæ which feed on plants or parts of plants in which the usual protective attitude would not avail.

THE PROTECTIVE ATTITUDE OF NOTODONTA ZICZAC AS AN INSTANCE OF SIMULATED ANGULARITY.—Truly angular attitudes are entirely impossible during prolonged rest for such soft-bodied, semicylindrical, organisms as caterpillars (with the necessity for the constant circulation of air and blood through their respective systems). Therefore the appearance of a very angular attitude is a protection, as

affording a great unlikeness to organic form as assumed in this division of the animal kingdom.

(There is often the additional protection of distinct likeness to some object which could be of no interest to the enemies of the larva).

Hence the not infrequent position of some structure on the convex side of a bend producing the effect of an angle. A most remarkable instance of this is seen in the attitude of *N. ziczac*, the name of which indicates that entomologists have been deceived as to the true position of the larva when at rest. This caterpillar throws itself into a series of undulations in the vertical plane, of which the bends are perfectly round and even, and yet by a structure to point each curve the appearance of an angular *zigzag* is produced.

The following is an account of the series of bends with the structures situated upon each:—The head and two succeeding segments are thrown backwards, producing a curve with the proximal part of the body. The 4th segment is in the centre of this curve, of which the convex side is, of course, situated ventrally, and it is distinctly pointed by the 3rd pair of true legs, which are held out straight in the protective position, and at once attract attention. The centre of the next bend (in the opposite direction) is the 6th segment, and its convex dorsal side is rendered very prominent by a large hump, which in this attitude completely dwarfs that on the 7th segment. The convex side of the next bend (in the 10th segment) is pointed by the 4th pair of claspers, which are held so as to be very conspicuous, and further attract notice by their strongly contrasted colours. The 2nd and 3rd pair of claspers have slight traces of a light longitudinal stripe, but the 4th has so large a stripe as to convey the impression that the lateral (spiracular) line is turned aside into it. Careful examination, however, shows that this is not the case, for the line can just be detected posteriorly to this point. The wide light stripe on the 4th pair of claspers also gains in prominence by the presence of another dark marking sharply contrasted with it, the two opposite shades of colour meeting in an abrupt line of demarcation, which traverses the external side of the clasper longitudinally. The dark stripe does not occur on the other claspers, and it is continued on to the posterior part of the 4th pair from the clouded orange-colour upon the 11th and 12th segments, of which colour it shows the deepest shade. It

cannot be doubted that the object of this striking effect and peculiarly prominent method of holding the claspers is to attract attention to the convex side of the bend, and to convey the notion of angularity. After this bend there is a very marked hump on the dorsal side of the 12th segment which suggests another bend, only represented, in fact, by a very slight downward curve; while the last pair of claspers aids the delusion by being directed downwards and backwards. (It may be noteworthy that these claspers still retain some slight functional value in this species). This last curve is also intensified to the observer in another way. After contemplating a series of curves the mind is ready to continue the series upon a very slight suggestion. This principle is frequently made use of in the markings of insects, and I have had occasion to allude to it in describing the markings of the genus *Smerinthus*. Thus in *N. ziczac* the eye is directed to the convex sides of all the curves, and the impression is conveyed that they are sharp and angular, that they follow the outline of the structures on the convex sides instead of the true outline of the larva. All the four curves are, in fact, quite smooth and gentle, and the last one hardly exists.

When the larva is crawling it is seen that very much of the effect is due to the prominent way in which the structures are held, for they are then hardly noticeable (except the humps on the 6th and 12th segments, and the former appears now on much more equal terms with that on the 7th segment).

On October 15th of the present year (1883) I found a full-fed larva of *N. ziczac* (feeding on *Salix rubra* near Oxford) which presented some differences from the normal form. It was much darker than usual; the spiracular line—really a little below the spiracles—was distinct on the 2nd and 3rd segments, then absent, reappearing faintly on the 6th segment, and increasing in distinctness on succeeding segments to the 10th. On the clasper of the 10th segment it formed a very prominent bright yellow stripe, bordered posteriorly by the dark colour of the posterior segments, here also darker than elsewhere. The spiracular line was completely turned aside into the clasper, and there was no trace of it posteriorly to this point. Dorsally the dark longitudinal patch on the 2nd, 3rd, and 4th segments is seen to be part of a regular dorsal line traceable up to and over the hump on the 12th segment, even down to the anal flap. The dorsal

line is bordered by lateral light lines. There is a slight subdorsal on segments 2, 3, and 4. On segments 5—10 inclusive there are oblique light stripes bordered anteriorly with a darkened ground colour, just as in *Smerinthus* larvæ, and sloping the same way.

NOTE UPON THE USE AND NATURE OF THE MARKINGS OF A NEMATUS LARVA (TENTHREDINIDÆ).—On October 14th of the present year (1883) I found a nearly full-grown larva of *Nematus curtispina* feeding upon sallow in the Oxford University parks, close to the Cherwell. The markings were all longitudinal and very simple, and are shown from above in Pl. I., fig. 8. There was a very dark green (almost black) dorsal line extending from the 2nd segment to within (apparently) two segments of the posterior end of the body. The posterior end of the dorsal line showed a slight dilatation, and the line was interrupted at the intersegmental rings. This dorsal line lay in the midst of a very distinct narrow white stripe stretching the whole length of the body (excluding the head). On each side of this the general green colour of the larva was shaded with black. There was a very fine but distinct white spiracular line, and there was a white ventral line. The head was yellowish brown, with a black curved line on each side. These were all the markings visible on the larva, and the ground colour was a transparent and yet dusky yellowish green. The larva, when found, was clinging closely to the edge of a semicircular notch in the leaf, due to its own exertions. Looked at from the side the larva was very inconspicuous, as the green colour resembled that of the leaf, and the longitudinal dorsal stripes were barely visible in profile, and what was seen of them rather aided the protection. If the larva habitually clung to the uninjured edge of the leaf it would be easily recognisable in profile, because it would stand out beyond the natural edge, and also would interrupt the serrations or other natural features. But, as far as I observed, the larva attached itself to the edge which it had been eating away, and this, too, was the most natural position, for it was thus quite close to the leaf and the part of the leaf upon which it was actually feeding; and in such a position the body of the larva did not attract any attention, for it was merely added to an artificial edge, and did not render the latter conspicuous. But the larva was protected by its colours and position, when seen from above, as well as in profile.

In the former case the white dorsal stripe (with its narrow dark central line) was not distinguishable from the edge of the leaf, except on a close inspection. The effect of the dark shading on each side of the white stripe was to produce an appearance of lateral compression, so that the thickness of the larva did not attract attention. The fine white spiracular line could not be seen from above, and was only visible from the side when it was carefully searched for. It seems to take no part in protection. At first I thought that this was merely an interesting case of protective marking, but a little investigation led me to suspect that the nature of the colouring was peculiar.

The fine dark dorsal line was certainly the dorsal vessel, and its pulsations were distinctly visible to the naked eye. It formed a darker line than I have seen (similarly caused) in other larvæ, and evidently in this case the skin was especially transparent. Carefully examining the white stripe with a lens I found that it had the peculiar lobed appearance of the fat body, and that it was moved by the pulsations of the dorsal vessel. Thus it was certain that the white stripe was also due to some internal part of the larva shining through the skin. Similarly, with the simple lens, I could distinctly see the tracheæ radiating from each spiracle, and I was led to believe that the fine spiracular line was merely due to the main longitudinal tracheal tube on each side. Dissection entirely confirmed all these suspicions, and showed that the only true coloration of the skin—caused by a pigment deposited in its own cells—was the black shading on each side of the white stripe. The general green colour is chiefly due to the fluids of the body, the contents of the digestive tract and the green colour of many of the tissues, notably those cells in which the deposition of fat is taking place.

We have here a remarkable instance of protective colouring due to internal organs. The case of the fat body is especially interesting. Apparently the first cells to become filled with fat globules, and to gain a white appearance, are arranged in two rows, one on each side of the dorsal vessel. But this process cannot be carried on indefinitely, or the white band would become too wide for protective purposes; and the massing of mature cells elsewhere would cause white colours to be seen through the transparent skin, if the massing took place

in any position except one. This one position is the median ventral line, and this was the only other place where mature fat-cells could be found. Here they were collected round the ventral gangliated nerve-chain, and formed the white ventral line. In this position they are, of course, completely invisible in all natural positions of the larva.

Cells partially filled with fat are very common in other parts of the body, but none of these appeared white by reflected light, and I have no doubt that such cells are only found along the dorsal and ventral line. This was certainly the case in the specimen I dissected, which was probably full-grown, as I had noticed some slight changes of colour indicating the nearness of pupation. The spiracular line is merely the result of an extremely transparent skin important in producing other markings, and the former is thus incidental to the latter. It seems very probable that in many other cases also natural selection has taken advantage of the ready-formed colours of internal organs to produce the markings of larvæ. Indeed, the effect of the dorsal vessel in this direction, and the intensification of a general green colour from internal causes, are already well known in many lepidopterous larvæ. I was able to name the hymenopterous larva described above from Cameron's monograph on the British phytophagous Hymenoptera (Ray Society, 1882). Mr. Cameron draws attention to the attitude of the larva at rest, when it clings close to the curved surface which it has eaten out of the leaf.

TWO KINDS OF PROTECTION BY RESEMBLANCE TO SURROUNDINGS, SPECIAL AND GENERAL.—In the well-known cases of protective mimicry the organism resembles more or less exactly some portion of its environment. Thus the larva of *S. ocellatus* is protected by resembling the under side of a curled apple leaf (when it feeds on this plant). Holding the larva in one hand and the twig in the other the resemblance is marked, and the observer is led to wonder at the protection afforded. This is *special protective mimicry*, and to the same class belong the numberless beautiful instances of protection familiar to us from our own observation or that of others. But there is another kind of protective resemblance to which less attention has been directed, which is less apparent although not less real. Holding the larva of *Sphinx*

ligustri in one hand and a twig of its food-plant in the other, the wonder we feel is not at the resemblance, but at the difference; we are surprised at the difficulty experienced in detecting so conspicuous an object. And yet the protection is very real, for the larvæ will be passed over by those who are not accustomed to their appearance, although the searcher may be told of the presence of a large caterpillar. An experienced entomologist also may fail to find the larvæ until after a considerable search. This is *general protective mimicry*, and it depends upon a general harmony between the appearance of the organism and its whole environment, so that the former does not attract attention. It is impossible to understand the force of this protection for any larva, without seeing it on its food-plant and in an entirely normal condition. The artistic effect of green foliage is more complex than we often imagine; numberless modifications are wrought by varied lights and shadows upon colours which are in themselves far from uniform. We are unable to appreciate the significance of larval colours apart from the food-plant, because we do not comprehend all the factors that combine to form the whole appearance of the latter. General protective mimicry is such an appearance in an organism that the artistic effect of its surroundings is sufficiently reproduced in it to prevent attention from being attracted when the one is seen in the midst of the other. A better instance of this general protection is seen in the larva of *Papilio Machaon*. Here the protection is very real when the larva is on the plant, and can hardly be appreciated at all when the two are apart. The terms I propose seem to express the difference between these two forms of resemblance, protection being gained in the one case by the production of a general effect, in the other by the acquisition of a special appearance. I am aware that general protective resemblances have been already appreciated, especially by Weismann, in the work to which I have alluded. I believe that this is the first attempt to separate the two, and to confer distinctive names upon them. As might be expected, the two classes are connected by intervening forms—by organisms that are protected in both ways. Thus the larva of *S. ligustri* has doubtless *some* special resemblance to a series of leaves, each leaf being represented by the green colour between two of the purple and white stripes.

But this is very different from the special resemblance of *S. ocellatus*, and the former larva would be very imperfectly protected were it not for the additional general resemblance.

The number of larvæ protected by general resemblance is very large. A very small class (comparatively) is protected by taste or smell, a still smaller class by the possession of terrifying markings, structures, attitudes, or movements. Those specially protected form a large class, and I imagine that all larvæ unprotected in one or more of these three ways are protected by general resemblance. The latter will, I believe, prove to include by far the largest number of instances. In many cases a larva may be *specially* protected upon one food-plant, and *generally* upon others. So also a larva may have been very specially protected upon its original food-plant, which may be now unknown.

These same terms also apply to other cases of protection, such as the mimicry of distasteful forms, or of forms otherwise protected (special protective mimicry). The same terms also apply to all organisms which avail themselves of protective shapes, colours, attitudes, &c.

THE SIGNIFICANCE OF LARVAL (AND PUPAL) DIMORPHISM.—Professor Weismann has proved that in many cases dimorphism is simply a phase of transition into monomorphism of a different kind from that which the species assumed before the commencement of changes which led to dimorphism. The whole transition from the first *monomorphism* is, he says, first *variability*; then *polymorphism*, produced by the comparative permanence of the favourable varieties; then *dimorphism*, by the predominance of the two most favourable forms; finally *monomorphism*, by the ultimate permanence of the one most favourable form. One of the forms in the stage of dimorphism is the old monomorphism, and the other is that which will become the new monomorphism. This theory is proved for many larvæ, but I believe that there are instances in which such an explanation does not hold. It is indeed probable that there are several explanations for as many forms of dimorphism. I will now allude to one instance, and will show some grounds for not accepting the above explanation of its cause, afterwards attempting to account for it in another way. The larvæ of some of the *Ephyridæ*, after the last ecdysis, are dimorphic, appearing in the two usual

colours, green and brown. (*E. orbicularia* is variable, *E. pendularia* regularly dimorphic, *E. omicronaria* dimorphic, with a great difference in the relative numbers of the two forms. Some, if not all, of the other species are also dimorphic, but I have not had the opportunity of observing them closely).

The interesting, and, as far as I know, unique, point about this dimorphism is that it extends into the pupal state, and thus seems to prove a permanence of the condition which is irreconcilable with Prof. Weismann's view. The brown larvæ always become brown pupæ, and the green larvæ green pupæ. I have never known an exception to this (see figs. 9 and 10 for the green and brown pupæ of *E. omicronaria*, figs. 11 and 12 for those of *E. pendularia*). There is, however, no extension of this pupal dimorphism into the imago stage. It has nothing to do with sex. This is shown by the following figures:—I possessed 43 pupæ of *E. pendularia* of the first summer brood of 1883. Of these 30 were green (producing 17 males and 13 females), while 13 were brown (producing 5 males and 8 females). Many of the next generation of pupæ also emerged, forming a second summer brood. Of these (40 in number) 27 were green (13 males and 14 females), while 13 were brown (7 males and 6 females). Furthermore, there is no distinctive mark by which it is possible to identify the imagines from either set of pupæ. Hence it appears certain that the larval and pupal dimorphism is of advantage in these stages only, and has no further significance in the ultimate stage.

This seems to be true of *nearly* all cases of dimorphism (although in some few instances it is sexual: see note to pages 308, 309 of Prof. Weismann's book). This advantage I believe to be a *direct* result of dimorphism. It is of value to a larva and pupa (if exposed) to be divided into two groups, coloured respectively with the two most protective tints. It is certainly a protection to the species against the keen sight of entomologists. It is well known by every collector of larvæ that it is often difficult to find a larva for the first time, but that after this it is comparatively easy to find more. In colloquial phraseology the eye "gets in" for that particular species. And I believe that this is true (although to a much smaller extent) for each day's work at larva-hunting. I think that everyone who has tried to find a larva, which he only knows by book description, upon its

food-plant, and, having succeeded, has gone on to find many more, will appreciate the great amount of truth that there is in the popular notion of the eye "getting in." The true explanation for this kind of work is, of course, that we can never appreciate the true relation of a larva (protected by colour, &c.) to its surroundings until we have had actual experience of it. This is especially true of the larvæ which depend upon general protective resemblance. And, having become once accustomed to the disguise in a particular instance (the reality of which is shown by the difficulty in getting accustomed to it) it is comparatively easy to detect other similarly protected instances. The reason why description can never take the place of experience has been shown in the discussion of "general protective resemblances"; it is because the harmony is so subtle that it cannot be understood without most careful observation of the perfectly normal and undisturbed larva on its food-plant. Even then, as was pointed out, although the disguise may fail before an experienced observer, the complex conditions which render it generally successful—in fact the disguise itself—may not be understood in the least. If this be true it is obviously an advantage to a larva to appear under two forms possessing respectively the colours which are most (generally) protective: an especial advantage if the colours are added to a form with much special protective resemblance. There is, in fact, a special protection for both forms, the yellowish-green larvæ resembling young green birch twigs, the brown larvæ resembling older twigs.

It is very likely that an entomologist who had never seen either form would continue finding the form which he first discovered, and would fail to see the others (after searching a tree twig by twig in the manner of the enemies of the larvæ). Or, if he found both forms, he would find one more easily and frequently than the other, that, namely, to which he was more accustomed, and he could not become as accustomed to either as he would have been to the larva if monomorphic. There might often be exceptions to this, but if it ever happened the species would gain by larval dimorphism. There is every reason to believe that the natural enemies of the larvæ are similar to man in the respect above-mentioned.

In other kinds of protection we argue from the effect produced by certain colours, forms, or attitudes upon

ourselves, to the effect that must be produced upon other animals, and by observation we can often prove that the inference is correct. I have before shown that if a marking be repeated so as to form a regular series the latter can be carried on by a mere suggestion of the further repetition of the same marking without producing any suspicion of imperfection. In this case we cannot doubt that the advantage gained is by bringing about a similar absence of suspicion in those animals which are the natural enemies of the organism. But in granting this we are committed to the belief that the mental organisation of animals is similar to that of man in this respect; that both are equally deceived by the suggested marking, because in both there is the same subjective readiness (so to speak) to continue the series. In the same way it is most probable that animals, in searching after a prey that is protected by colour, &c., are likely to continue finding those that they first come across in any particular hunt. And this fact would be of especial value as against those enemies that seem to systematically work over a whole tree.

To put the argument perfectly plainly, I think all will admit that the larvæ upon a tree stand a better chance against their various enemies if they belong to two differently coloured species (both well protected) than if they are all the same. So dimorphism is an advantage when the divergence in colour is quite complete. Again, a large number of larvæ of one colour attracts attention and multiplies the chances of detection, and increases the danger for all. This is especially true of the larvæ of small moths laying their eggs upon isolated trees, for there are likely to be a great many larvæ upon one tree under these conditions. Without pressing the analogy too far between man and the natural enemies of larvæ, I think we may admit that larval dimorphism may be of direct value to a species in the manner indicated above. If this is the case the dimorphism will continue as a permanent condition unless there is a great difference between the protective values of the two forms.

I obtained twenty-eight pupæ from eggs from a female bred from the brown form and fertilised by a male similarly bred. Of these twenty-eight exactly half were brown and half green. In this case the number of brown forms is much above the average, and it is probable that the proportion could be increased

by again breeding from the brown forms. If in any district the green forms were especially attacked the greater proportion of brown ones left would increase the number of larvæ whose parents were both brown,—in other words, would greatly increase the proportion of brown larvæ in the next generation. But this would bring the brown larvæ into prominence, and would render it more probable that they would be especially attacked, and so the disproportion would right itself. According to this argument there should be a tendency (apart from the effect of enemies) for the more abundant form to predominate, owing to the greater chance of eggs being fertilised and laid by individuals of the same form. It is possible that there is such a tendency, and that such a result is coming about (in this case the gradual predominance of the green), but I think that this is hardly likely, and there are indications that the problem is very complex. There is no doubt that green is the better protective colour for summer and brown for autumn and winter. In the first summer brood there were 30 green and 13 brown; in the second there emerged 27 from green pupæ and 13 from brown (and these numbers include 5 brown and 5 green, from the lot of which both parents were brown, hence unduly raising the average of the latter).

There remained 34 pupæ of the second brood, of which 15 died, while 19 will (probably all) emerge in the spring. The 15 belong to the group which emerged last summer, for they died just before emergence, with the colours of the wings plainly visible through the pupal covering. Of these 15 pupæ 10 were green and 5 brown (including 5 green and 3 brown from the lot with brown parents). Of the remaining 19, which form the true winter brood, 12 are brown and only 7 green (including 4 green and 6 brown from the lot with brown parents). Hence in the last case only, the proportions are reversed, and there are nearly twice as many brown pupæ as there are green, while there were more than twice as many green pupæ in both summer broods. I hope to make further observations upon this point, but there seems to be much reason (from these statistics) for believing that the brown forms predominate when brown is the best protection, and green forms when green is the best protection. It is noteworthy that the colours appear first in the larvæ (always corresponding with those of the

pupæ) which all feed up together, those namely which will emerge the same summer, forming the beginning of a second summer brood, and those which will emerge next spring and belonging to the old winter brood.

I made some observations upon the situations selected for pupation, thinking that these might show some relation to the colours of the pupæ. Of those I observed 11 brown pupæ and 20 green were fixed to leaves; 4 brown pupæ and 6 green were fixed to twigs; 10 brown pupæ and 8 green were fixed to the case in which the larvæ had been kept (the latter having wandered from their food-plants). The wandering larvæ are more likely to represent those which would have been normally fixed to twigs. The statistics seem to point towards some possible relation, but they are not convincing; and, in fact, the protection of a (yellowish) brown pupa upon a leaf and of a green one upon a young twig is very considerable. Again, some leaves bearing pupæ would fall off and turn brown. I hope to make further observations upon this interesting question, and to investigate the phenomenon in other species of *Ephyridæ*. I should have added that I can draw no conclusions as to *E. omicronaria* for want of sufficient material. I had 12 pupæ (11 green and 1 brown), and it is probable that the above conclusions have applied here, but that the brown form has almost disappeared. There is not the same reason for an alternate predominance of the two colours at different seasons (in the pupæ) because *E. omicronaria* was, at any rate in 1883, very slightly double-brooded. Only one of the 12 pupæ emerged. This less marked tendency to double broods may render it more likely that the green forms should predominate. Thus, in *E. pendularia* the dimorphism is of direct value to the species in two ways, by giving an extra chance of escaping detection, and in the fact that the more protective colour predominates at the appropriate season of the year. It may be suggested that the latter gain is so palpable that it is probable that the larva is progressing in that direction, *i. e.*, towards a true seasonal dimorphism. But I believe that a certain proportion of brown (larvæ and pupæ) in the summer, and a certain proportion of green (pupæ) in the winter, add to the safety of the species; and further, the larvæ which produce the winter pupæ feed in the late summer, when green is an obvious protection. Hence the predominance of brown must be

entirely for the protection of the exposed winter pupæ, and, as has been shown, the predominance is only manifested by that proportion of the second generation of larvæ (in the year), which will form the winter pupæ. It is strange that the imagines of *E. omicronaria* should show distinct seasonal dimorphism, and yet that only a small proportion should emerge as the summer form. On the other hand *E. pendularia* (imago) shows indistinct seasonal dimorphism, and has two summer broods. It is probable that there is a considerable summer brood of *E. omicronaria* in more favourable years.

PHYLETIC PARALLELISM IN METAMORPHIC SPECIES.—Prof. Weismann's valuable essay on this subject (in the work previously referred to) proves that the different stages of two great groups may not show an equal divergence or affinity. He shows that the grouping would in many cases be entirely different according to the stage which is selected as the criterion of divergence, and further, that this varying divergence depends upon a corresponding difference or agreement in conditions. He proves these propositions from Diptera, Hymenoptera, and Lepidoptera. With regard to the latter he shows that the division into butterflies and moths depends upon imaginal characters, while the larvæ do not manifest an equal divergence. It is not possible to arrange the larvæ of Rhopalocera together in one great group as it is possible to arrange the imagines. And this imaginal divergence is accompanied by a difference of conditions, for butterflies *as a whole* live under very different conditions from moths *as a whole*. On the other hand, the want of divergence between the corresponding groups of larvæ is accompanied by a similarity of conditions. (On the other hand he points out that the larvæ of Rhopalocera can be divided into smaller groups corresponding with imaginal classification).

It seemed to me that it is worth adding a note about the pupæ to this most important comparison, for which we are indebted to Professor Weismann. The pupæ of Rhopalocera can be formed into a large group corresponding to the union of the imagines into one of the two chief divisions of Lepidoptera. The characters by which these pupæ can be identified *as a whole* are bright, or at any rate varied, colours; angularity of outline,

especially anteriorly; and mode of suspension. The divergence from the pupæ of Heterocera as a whole is also accompanied by a difference in conditions; the latter being protected from light in the earth or in cocoons, while the former are freely exposed to it. The natural colour of the chitinous pupal covering, *i. e.*, that colour which needs the least constructive energy for its formation, seems to be red-brown. This is the common colour of pupæ which are shut up in opaque cocoons (as *D. vinula*, &c.), where the colour can be of no importance. It is, however, a positive advantage to those species which pupate in, or upon the surface of, the earth. Hence this colour is almost universal among the pupæ of Heterocera, being of direct (protective) or indirect (by saving energy) advantage to nearly all of them. One group of exceptions is very significant, *i. e.*, the colours, &c., of the pupæ of *Ephyridæ*. These Heterocera pass the pupal state under the same conditions as those of Rhopalocera, freely exposed to light and air, suspended by a band round the body, and by a pad to which the posterior spine is attached. The conditions are thus the same as those of Rhopalocera. (The suspension, *i. e.*, the way in which the condition of exposure is attained, is identical with that of many pupæ of Rhopalocera). Corresponding with these similar conditions the pupæ of *Ephyridæ* possess bright colours (Pl. I., figs. 9—12), and are anteriorly angular. The bright colours depend upon the transparency of the chitin, which allows underlying tints to shine through. Hence in these pupæ the colours disappear shortly before the appearance of the imago, and the markings and colours of the latter gradually become completely visible. This is also true of Rhopalocera as a whole. The bright colours in these cases are of protective value, either by special or general resemblance. The red-brown tint is not a good protection, except in the situations mentioned above. The warning colours of distasteful pupæ are very different to the bright protective colours of the pupæ referred to (*e. g.*, compare the pupa of *A. grossulariata* with those of the *Ephyridæ* or Rhopalocera).

It thus appears that the pupæ of Rhopalocera form a chief group corresponding to the imagines, and that the differences from the other chief group of Heterocera are in both cases accompanied by a divergence in the respective conditions. The angular outline must also

be a result of the same conditions. There is no doubt that this outline is protective, or has been descended from a protective ancestral character, and such protection by an angular outline, of course, follows from the fact that the pupæ are freely exposed. These facts are true of the pupæ of *Rhopalocera* as a whole, but there are exceptions, just as in the imaginal characters.

EXPLANATION OF PLATE I.

FIG. 1.—Natural size. Adult larva of *Smerinthus ocellatus*, seen from the left side. The ground colour is bright yellowish green, and the three rows of red spots are seen to form an alternate pattern, the spots of the highest row being placed nearly vertically over those of the lowest; while the middle spots are approximately intermediate. The anterior remnant of the subdorsal is normal. The slight oblique stripe anterior to the seven-stripe system is indicated. The shagreen dots are arranged in rings parallel with the intersegmental furrows, and there are generally eight rings in the larger segments. The anterior borders of the oblique white stripes are darker green than the ground colour.

FIG. 2.—Natural size. Apparently adult larva of *S. populi*, seen from the left side; from a painting by Mr. G. C. Bignell. The larva is remarkable in its light ground colour, and especially in the extreme development of the red spots, which are continued anteriorly, where there are no oblique stripes, and the spots have no tendency to become drawn out into coloured borders. They are rather feebly developed on the claspers. Anteriorly they are not distributed regularly on the segments, since they exceed the latter in number. The alternate arrangement is less marked than in the last figure. This unusually-marked variety does not bear out Prof. Weismann's theory that the spots tend to become drawn out into coloured borders to the light stripes, and yet here the system of spots reaches a far higher development than in *S. tilie* (as far as I have seen figures of the variety of this species).

FIG. 3.—Natural size. Rather exceptionally large adult larva of *S. ocellatus*, from the left side. The ground colour is light bluish green. No red spots are present, but there is the normal red line round each spiracle. The subdorsal is retained for its whole length, although but faintly, posteriorly to the normal limits. It ends posteriorly in the last oblique stripe (the limit shown in an earlier

stage of the ontogeny). The small 8th oblique stripe is shown. The ground colour is darker in front of the oblique white stripes.

FIG. 4.—Natural size. The head and anterior segments of the same larva as Fig. 3, seen from the left side in the *Sphinx* attitude of repose. The spiracle on the 2nd segment is nearly hidden among the folds due to the attitude. The anterior part of the subdorsal is bent down into approximate parallelism with the oblique line system. It is seen that the latter system would have been marred if it had been repeated anteriorly with the same relation to the segments that it possesses posteriorly. The slight 8th stripe deepens the impression that the subdorsal belongs to the oblique system. The effect is less complete in this figure than in the normal larva, because the subdorsal does not disappear posteriorly in this particular larva.

FIG. 5.—Adult (and probably enlarged) larva of *Endromis versicolor*, seen from the right side, copied from the plate on page 203 of Newman's 'British Moths.' The horizontal spiracular or subspiracular line seems to be normal on segments 2—6. Posteriorly to this point it becomes oblique on each segment, forming a line with the (true) oblique stripe of the segment in front. The older marking is thus completely subordinated to the more recent system, except where the latter is absent (segments 2 and 3), or but little developed (segments 4 and 5). The older form of marking is easily recognised, even in the segments in which it has been modified, by a single row of longitudinally arranged dots always present upon it, but absent from the true oblique system.

FIG. 6.—Natural size. Some segments of a nearly full-grown larva of *Sphinx ligustri*, seen from above. The slightly-marked dorsal line is due to the dorsal vessel. Each oblique white stripe passes into a yellowish green line posteriorly (as it reaches the limits of the segment in which its chief course lies). Each purple border similarly passes into a dark green line. The short yellowish green and dark green lines much resemble the colouring of the oblique system in *Smecrinthus* (yellow in *S. populi*, &c.), and suggest that this was the primitive marking.

FIG. 7.—Natural size. The posterior segments of a larva of *S. ligustri* fairly advanced in the last stage, seen from the right side. (The larva was the same as that shown in Fig. 6, but this figure [7] was made previously). The same relation of the pure white and purple stripes to yellowish green and dark green lines is seen from the side. Each white stripe becomes scattered and shagreen-like anteriorly and inferiorly. The purple border becomes darker anteriorly and inferiorly, and is continued on the posterior side of the white stripe (inferiorly) as a dark blotch. On the 12th segment there is a slight indication of a white stripe, and a considerable, though interrupted, purple line.

FIG. 8.—Natural size. Larva of *Nematus curtispina*, probably nearly full-grown, seen from above. In the middle line is the black (dark green), posteriorly dilated, dorsal line caused by the dorsal vessel. It does not extend to the posterior end of the body, and its continuity (as a line) is broken by the intersegmental furrows. This line is situated in a white stripe, which was seen to move with the pulsations of the dorsal vessel, and to be lobed, like fat-tissue. It is caused by a longitudinal accumulation of the cells of the fat body shining through the transparent skin. Outside this there is true black pigment in the skin, forming a dark line on each side, and beyond this the ground colour is green, chiefly due to internal tissues and fluids. Laterally (not seen here) a fine spiracular line is formed by the main longitudinal trachea shining through the skin. Thus all the colours and markings, except the black shading, are due to internal structures. The protective resemblance is to the edge of the leaf to which the larva clings, and the effect is increased by the appearance of lateral compression caused by the dark shading.

FIG. 9.—Natural size. The pupa of *Ephyra omicronaria* (green form), attached to a twig of maple.

FIG. 10.—Natural size. The pupa of *Ephyra omicronaria* (brown form), attached to a twig of maple.

FIG. 11.—Natural size. The pupa of *Ephyra pendularia* (green form) attached to a twig of birch, after the manner of the pupa of a butterfly (by a band round the body, and a pad to which the anal spine is fixed). The bright colours and the pair of anteriorly-placed angular projections give to the pupæ of the *Ephyridæ* an appearance singularly like those of butterflies.

FIG. 12.—Natural size. The pupa of *Ephyra pendularia* (light brown form), attached to a twig of birch.